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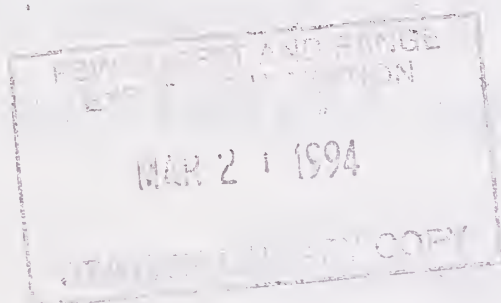
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# Initial Growth, Development, and Clonal Dynamics of Regenerated Aspen in the Rocky Mountains

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## **Abstract**

Root connections and clonal behavior was studied in 1-14 year-old developing aspen. Functional connections remained through age 14. Stem and root node density declined exponentially over time. Biomass and leaf area increased sharply at age 8-14. Growth was dependent upon crown position. Ramet populations were strongly aggregated.

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## Introduction

Quaking aspen (*Populus tremuloides* Michx.) growing in the western United States is one of the largest clonal organisms to be found on the planet. Individual aspen genotypes can cover several hectares and ramet generations may persist over 150 years (Shepperd 1981).

Aspen reproduces by asexual root suckering when overstory stems are removed or die (Schier et al. 1985). New ramets arise on roots within 0.15 m of the soil surface (Schier and Campbell 1978). Stems along one lateral root may initially be connected through a stump to other roots of the parent ramet (Jones and DeByle 1985; DeByle 1964). These connections become broken or nonfunctional as suckers develop their own roots (Zahner and DeByle 1965). Some functional connections between ramets arising from the same parent root do persist (DeByle 1964; Maini 1968; Tew et al. 1969). The influence of these connections upon stand development is not known.

Pitelka and Ashmum (1985) observed an extensive variation among clonal species to the extent in which root connections remain functional and in the patterns of movement of materials shared between ramets. They speculated that connections between ramets should depend upon the strength and distance between source and sink, and may help ramets overcome unevenly distributed resources, or enable a genotype to monopolize an occupied area. In some species this includes the ability to avoid self-thinning among connected ramets (Harper 1985).

Aspen does appear to exhibit some of these characteristics. Rapid and profuse aspen ramet production often results following catastrophic destruction of a previous ramet generation by fire, disease, or clearfelling. However, stem numbers rapidly decline within a few years after initial establishment. This phenomenon has been attributed to competition among young aspen and their susceptibility to a number of damaging agents (Crouch 1986; Hinds and Shepperd 1986), but might also be due to changes in the degree of clonal integration among ramets.

Not all young aspen populations are dense, however. Sparsely stocked, open grown stands also occur. Sparse stocking has been associated with a high incidence of browsing, snow damage, and fungal diseases (Hinds and Shepperd 1986). The extent to which sparse stocking affects the growth and development of young aspen populations is not known.

This research effort examined the density, aggregation, crown stratification, and stem growth of 1- to 14-year-old aspen ramet populations to answer several questions about the role of root connections and clonal behavior in developing aspen populations:

- How common are functional root connections in aspen clones that have been regenerated by a clearfelling harvest and how long do they persist?
- Does vegetative regeneration affect the spatial arrangement, growth, and competition among young aspen ramets?
- If so, do the growth and competitive processes differ between sparse and densely stocked ramet populations?

## Methods

Young aspen populations were sampled at five locations in western Colorado during the summer of 1989. The sites were located between 37.5° and 40.5° north latitude and 106.5° and 108.5° west longitude, in pure aspen forests that had been commercially harvested by clearfelling. All of the locations were of good site quality and between 2600 and 3200 m elevation.

Commercially harvested sites were chosen for several reasons: they were accessible, the original stands were known to be uniformly stocked pure aspen populations, and the complete clearfell harvest represented a uniform regeneration treatment that had been similarly applied from site to site over time. Ramet populations in the 5 areas ranged from 1 to 14 years of age. Most of each area was densely stocked and had complete crown closure between ramets, but each site also contained sparsely stocked areas that had numerous gaps within the canopy.

Three randomly oriented 0.2-m wide belt transects were established within an area of dense stocking and three within a sparsely stocked location at each site. Each location appeared to be a single genotype, based on stem and leaf characteristics. Transect length varied from 2-30 m and was predetermined according to population density and age with the goal of sampling 50-100 stems per transect. Resulting sample sizes ranged between 44 and 166 stems per transect. A total of 30 transects were sampled at the 5 sites.

The height, basal diameter, crown class, length of current year's terminal leader, and number of primary



branches were recorded for each stem, along with its distance from the beginning of the transect. Each stem was also assigned a root node number. Stems arising from common root nodes were assigned the same node number. Dead terminal leaders (along main stem axis only), stem and basal wounds, primary branches affected by browsing, diseased branches, and stem cankers were also noted.

Within each transect, a representative dominant, co-dominant, intermediate, and suppressed stem was cut at ground line for biomass determination. Stems and leaves of these 120 ramets (4 stems \* 3 transects \* 2 locations \* 5 sites) were weighed in the field, and subsamples from each stem were oven dried. Fresh weight/dry weight ratios of the dried subsamples were first used to calculate total dry weights of the 120 dissected stems. Those weights were then regressed against basal stem diameter to predict dry weight for all stems measured in the transects:

$$\text{Dry weight(g)} = 59.9517 * \text{Basal Diameter(cm)}^{2.521}$$

Estimated  $r^2 = 0.97$  S.E. = 795.34 g

A video scanner was used to measure the projected area of 2834 randomly selected leaves to determine a ratio of 0.008414 m<sup>2</sup> leaf area per gram leaf dry weight (S.E. = 0.0322 m<sup>2</sup>). This relationship was used to calculate projected leaf areas for the 120 dissected stems which were in turn regressed against basal diameter to estimate projected leaf area for all stems:

$$\text{Leaf area(m}^2\text{)} = 0.00015656 * \text{Basal Diameter(mm)}^{2.28215}$$

Estimated  $r^2 = 0.96$  S.E. = 0.276 m<sup>2</sup>

The occurrence and longevity of functional root connections between aspen ramets were investigated in a second experiment conducted during July and August of 1989 in eight additional regenerating clearfelled areas in western Colorado. These areas were separate from those described earlier, but in the same general locations. Forty-eight randomly selected aspen stems were isolated from neighboring stems with plastic sheeting and sprayed with over-the-counter premixed concentrations of two different commercial herbicides: Roundup<sup>2</sup> (Glyphosate, n-phosphomethyl glycine) and Weed-B-Gon (2,4-dichlorophenoxyacetic acid). Populations in the 8 sites were 1, 3, 7, 8, and 14 years of age. Stems of all sizes and crown classes were selected for treatment except in the 14-year-old population, where overstory stems were too large to be effectively treated.

At the end of the growing season, roots between sprayed stems and any nearby stems showing herbicide symptoms were excavated to verify a root connection. Height, basal diameter, crown class, and number of

primary branches were measured for all stems as well as the distance and average root diameter between treated and connected stems.

## Results

Root suckering enables aspen to establish quickly and grow very rapidly compared to sexually reproducing conifers in similar montane and subalpine climates. In contrast to germinating conifer seedlings, the number of aspen ramets in a population does not increase over time to a maximum. Rather, the maximum ramet density occurs immediately following regeneration. One of the most striking features of the young aspen studied here was the precipitous decline in the number of stems in dense ramet populations between 1 and 3 years of age (fig. 1). Density of these populations dropped from an average of 1.4 million stems/ha at age 1 to under 200,000 stems/ha at age 3. This decline in stocking continued to follow an exponential decrease over time.

$$\text{Stems/ha} = 1,382,937 * \text{Age}^{-1.85105}$$

Estimated  $r^2 = 0.96$ , S.E. 106,600 stems

Although regenerated aspen harvest units often have the outward appearance of being stable populations of dense, uniformly spaced plants, data collected in this study do not support the analogy. Stratification of the canopy within the study populations became much more distinct as stands increased in age (fig. 2). Average stem height increased linearly over time with dominants increasing in height at a faster rate than subordinate crown classes. However, average heights did not significantly differ between age or crown classes, except in the 8- and 14-year-old stands (fig. 2).

Average dry weight per hectare exhibited a similar pattern of rapid increase in 8- and 14-year-old stands.

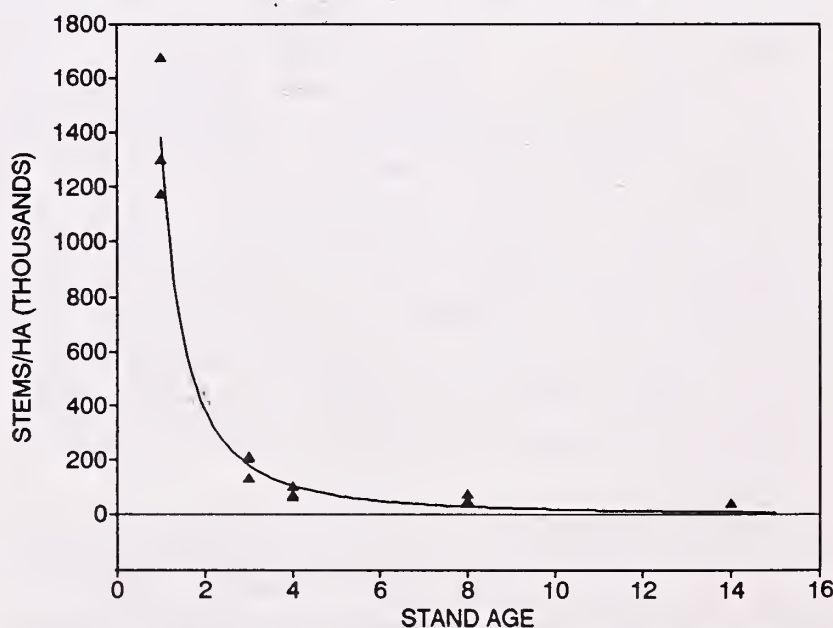


Figure 1.—Average stem densities among densely stocked aspen sucker populations in western Colorado declined at an exponential rate as stands aged. Densities fell rapidly from age 1 to 3, then decreased at a much slower rate at older ages.

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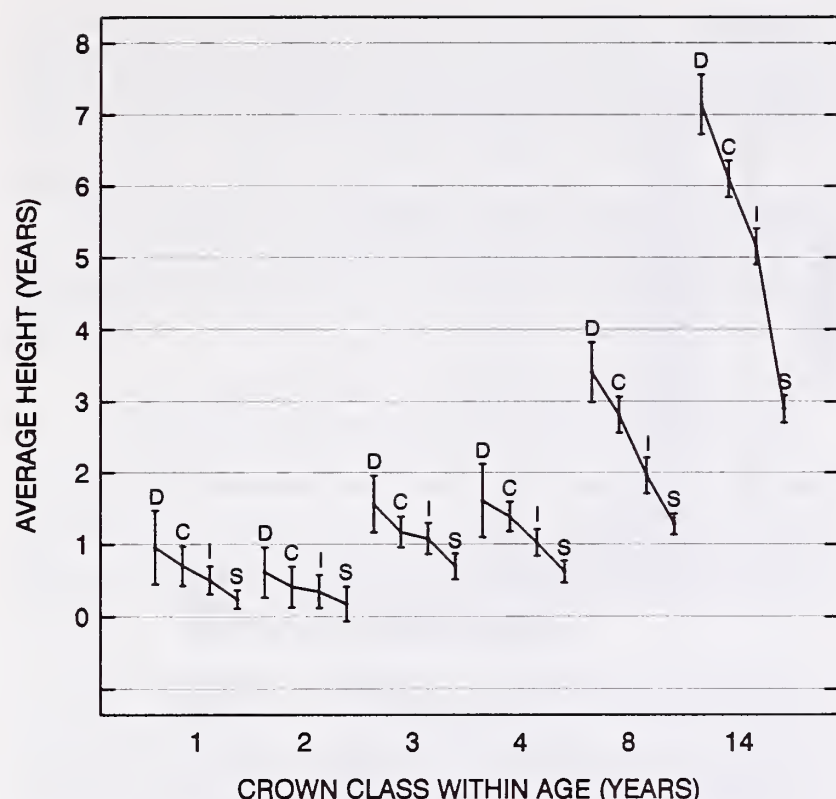


Figure 2.—Two-way analysis of variance of the heights of 777 young aspen stems sampled in 6 western Colorado aspen populations, 1-14 years of age. Bars are 95% Tukey HSD intervals for heights grouped by crown class and population age. Those within each age group which overlap in a horizontal plane are not significantly different. Crown class codes are: D = Dominant; C = Co-dominant; I = Intermediate; S = Suppressed.

Dry weights remained below 4500 kg/ha in dense 1- to 4-year-old transects and were not significantly different among age classes. However, dry weights increased significantly ( $p=0.05$ ) to 13,100 kg/ha in 8-year-old stands and to 32,500 kg/ha in 14-year-old transects.

Mean leaf areas per stem were also not significantly different among age and crown classes in younger stands, but increased sharply in 8- and 14-year-old populations, especially among dominant and co-dominant crown classes (fig. 3). The same pattern occurred among leaf area indices (LAI) of the densely stocked populations (fig. 4). Average LAI's were 0.58, 0.75, and 0.47  $m^2/m^2$  for 1, 3, and 4 years, but increased to 1.9 and 4.0  $m^2/m^2$  at 8 and 14 years.

A much different pattern was evident for mean current year (1989) leader growth. In this case, new leaders grew fastest in 1- and 2-year-old populations, then slowed among older populations (fig. 5). Differences in leader growth between crown classes were much more distinct in 1- and 2-year-old populations than in older populations.

In spite of their contrasting appearances, dense and sparsely stocked transects at each of the five locations contained similar numbers of dominant and co-dominant stems. Subordinate stem numbers were responsible for the obvious differences in stocking. Dense transects contained more suppressed trees per unit area than sparse populations in each of the age classes sampled.

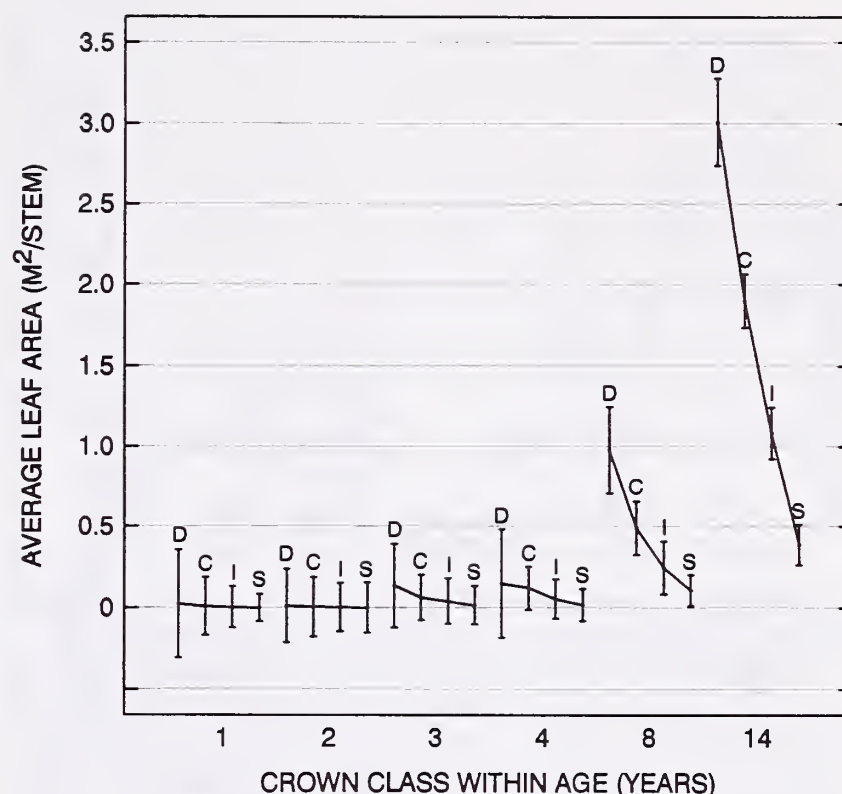


Figure 3.—Ninety-five percent Tukey HSD intervals for a two-way analysis of variance of mean leaf area by crown and age class for the 777 young aspen stems described in fig. 2.

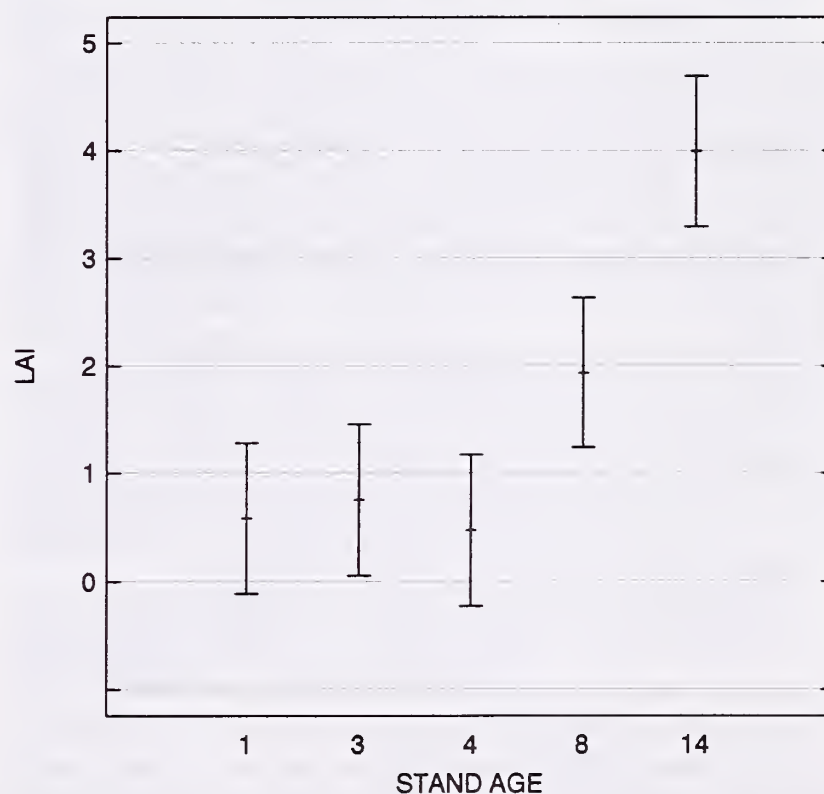


Figure 4.—Ninety-five percent Tukey HSD intervals for mean leaf area index (LAI) of dense aspen ramet populations by stand age class. Bars which overlap in a horizontal plane are not significantly different.

The presence of additional subordinate stems apparently stimulated height growth in dense stands. The 273 stems sampled in sparse populations were compared to the 504 stems sampled in dense populations using analysis of variance with age as a covariate. Stems in dense populations were significantly ( $p=0.05$ ) taller (2.13 m versus 1.44 m), and had longer leaders (0.25 m versus 0.22 m).

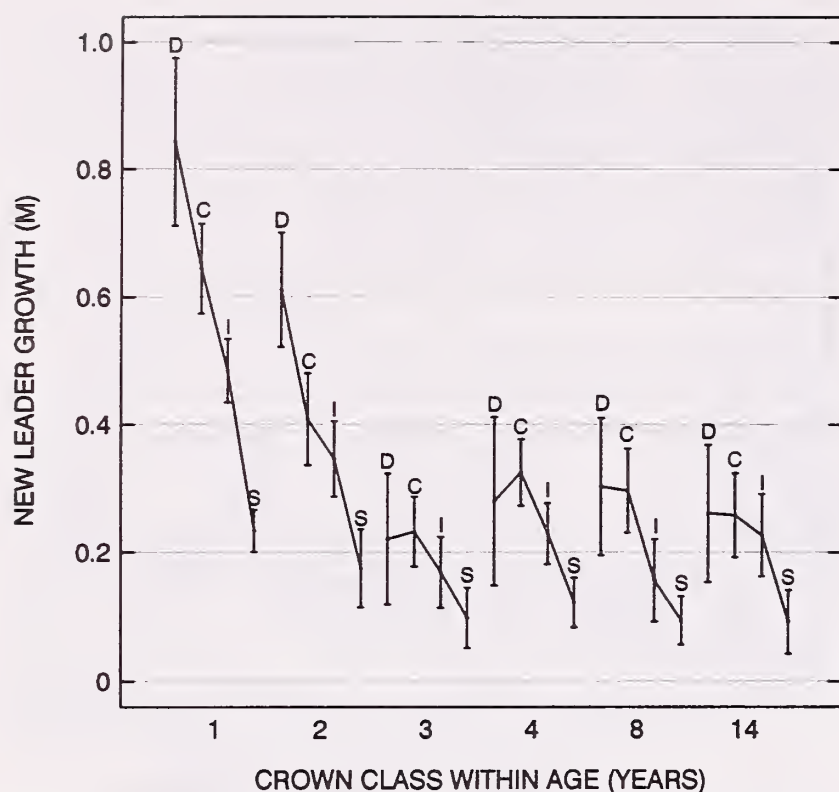


Figure 5.—Ninety-five percent Tukey HSD intervals for a two-way analysis of variance of new leader growth by crown and age class for the 777 young aspen stems described in fig. 2.

The incidence of herbivory-related damage also differed between stems in sparse and dense populations. Browsing was readily apparent in current year foliage and was significantly greater ( $p=0.05$ ) among stems in sparse populations. Stems in sparse populations averaged 0.7 browsed branches versus 0.07 browsed branches per stem in dense populations. Although there were more stems in dense populations, the number of browsed branches per unit area was still greater in sparse populations. These areas averaged 8100 browsed branches/ha versus 3150 browsed branches/ha in the dense stands ( $p=0.05$ ). The number of browsed branches declined somewhat in older stands, but there was no significant difference in browsed branches/ha among the age classes sampled.

Although many young aspen stands appear uniform, stems were aggregated in all the populations studied here. Descriptions of the spatial distributions of the aspen stem populations were obtained by calculating the distances between neighboring stems along each transect. Spacing of stems was tallied by 0.05 m classes and tested for aggregation using a variance/mean ratio (V/M) test described by Pielou (1977). There is no test of significance for the V/M ratio, but Pielou (1977) states that a population distribution is considered random with this test if "its V/M is near 1." The test indicated all populations in the study were aggregated, but the degree of aggregation diminished from a V/M of 60.0 at age 1 to a V/M of 5.4 at age 14.

Frequency distributions of the 0.05 m spacing intervals were plotted for 1- and 14-year-old populations (fig. 6). In both cases the distributions are skewed away from

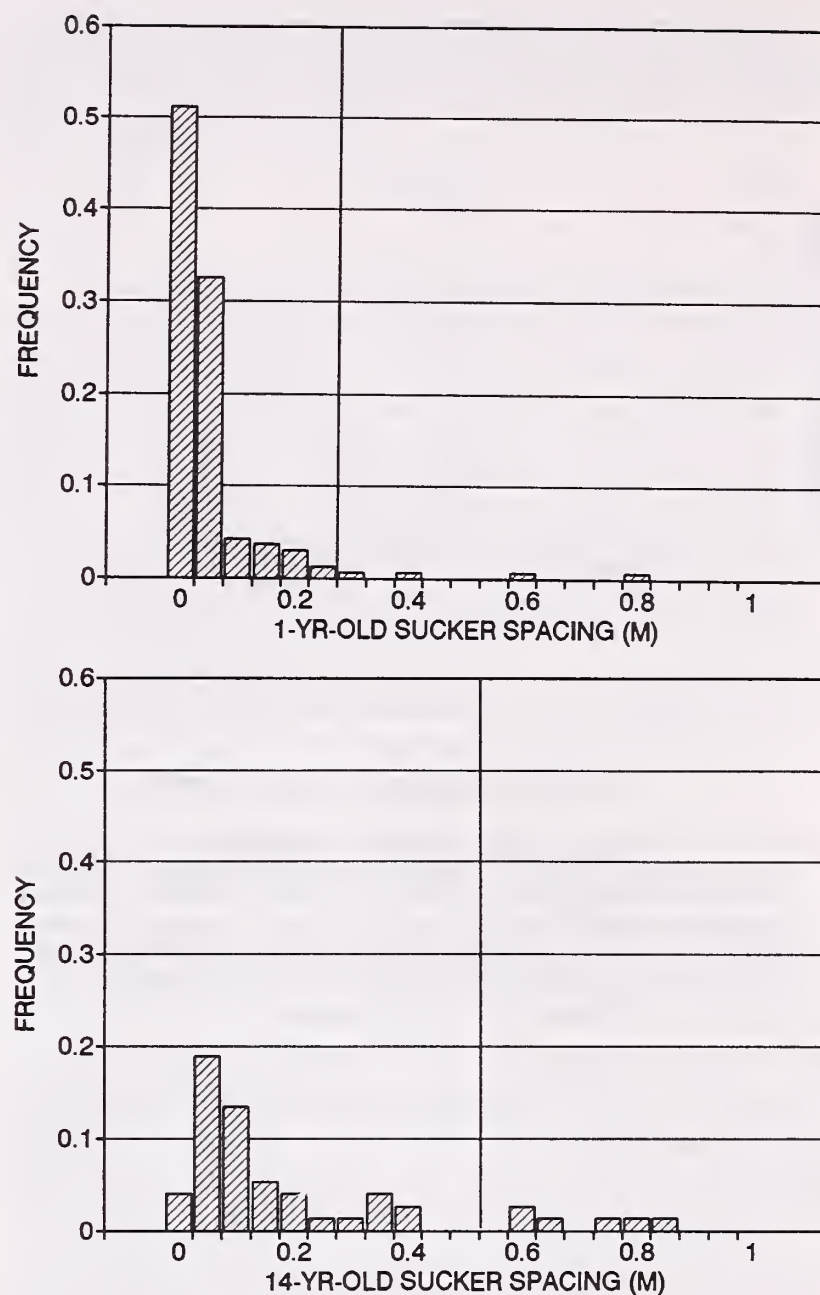


Figure 6.—Frequency distribution of 0.05 m stem spacing classes for 1- (upper) and 14-year-old (lower) aspen sucker populations. Each bar represents the portion of the total stems sampled that occurred in a spacing class. The zero class represents suckers arising from the same location on a root node. The vertical line is placed at the spacing interval of a uniformly distributed stand of the same density.

a line representing the median spacing of a uniform population of the same density. About half of the stems measured in 1-year-old transects occurred as twin stems (the zero class in fig. 6) and another third of the stems were within 50 mm of each other. Although mortality reduced the proportion of twin (zero class) stems in the 14-year-old transects, about 25% of the stems remained clustered within 50 mm of each other.

The degree of aggregation between dense and sparse populations of each age class was compared using David and Moore's (1954) Index of Clumpiness. Sparse transects were significantly less aggregated than dense transects only in the 8- and 14-year-old populations ( $p=0.05$ ).

Much of this aggregation may be attributed to multiple stems arising from the same root node. One-year-



old transects averaged 3.9 stems/node, but 3- to 14-year-old transects averaged only 1.7-2.1 stems/node (significant at  $p=0.05$ ). There was no significant difference in the average stems/node in dense versus sparsely stocked transects.

In contrast, the number of nodes per hectare observed in dense transects decreased exponentially as stands aged, similar to the decline in stem density (fig. 7).

$$\text{Nodes/ha} = 316,383 * \text{Age}^{-1.2211}$$

Estimated  $R^2 = 0.88$  S.E. = 41,693 Nodes/ha

There were considerably fewer nodes per hectare among transects placed in young, sparsely stocked populations (fig. 7), but no significant difference in node density between dense and sparsely stocked transects beyond age 2.

Not only were suckering root nodes more dense in young populations, they were also more highly aggregated than in older stands. V/M ratios for a frequency distribution of 0.2 m node spacing intervals ranged from 25.0 in dense 1-year-old stands to 2.2 in dense 14-year-old stands. David and Moore's (1954) Index of Clumpiness indicated that nodes in sparsely stocked transects were significantly ( $p=0.05$ ) less aggregated than those in dense transects in all but the 8-year-old age class. V/M ratios dropped below 2.0 by age 3 in sparse stands and remained below 2.0 through age 14, indicating that root nodes were essentially randomly distributed in those populations (Pielou 1977).

Root connections between suckers other than those among stems sharing a root node were also observed.

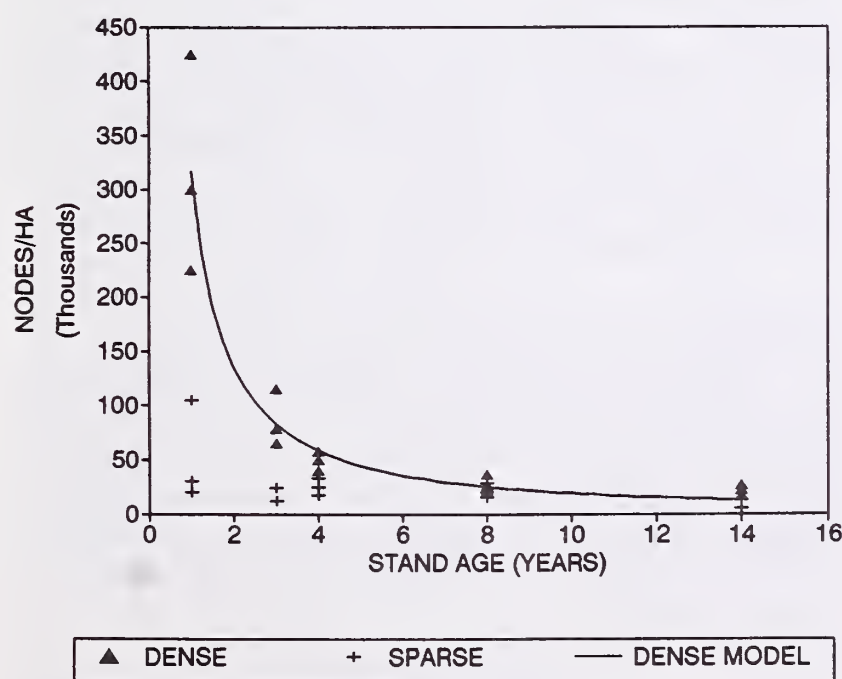


Figure 7.—The density of suckering root nodes declined exponentially with increasing stand age among transects in the five dense populations that were measured. Node density in sparse stands was initially much less than that of dense stands, but beyond 2 years of age, there was no significant difference ( $p=0.05$ ) in node density between dense and sparsely stocked transects. Plotted line is the exponential model fit to dense transect data.

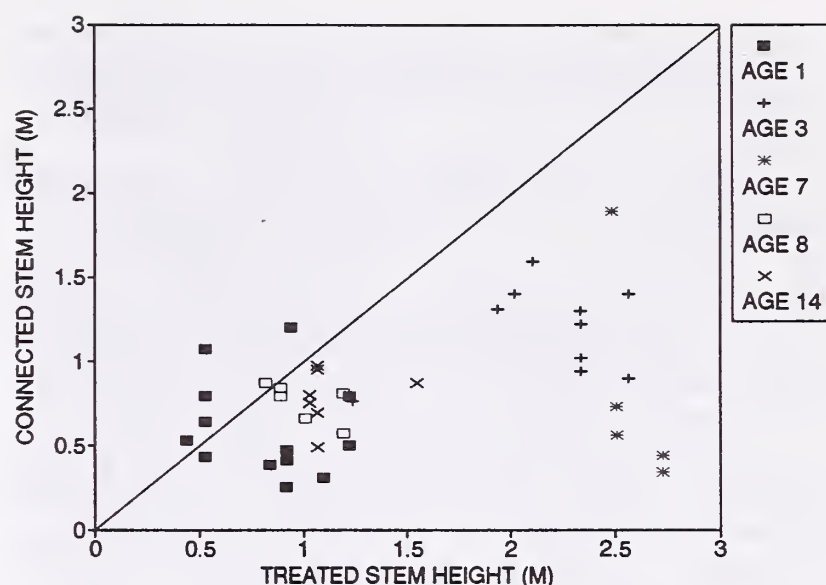


Figure 8.—Height of stems treated with herbicide versus those with functional root connections to them. Points below the diagonal line indicate instances where connected stems were smaller than treated stems.

The herbicide applications were able to identify such root connections in spite of a variable response to the herbicide treatment. Only 23 of the 48 treated aspen stems (48%) showed symptoms of the herbicide treatment. Since a water carrier was used with the herbicide, rain may have washed herbicide from some treated stems.

A total of 42 untreated stems were affected by the herbicide and were found to be connected to the 23 treated stems (1.83 connections per treated stem). Because glyphosate is readily translocated to roots (Fedtke 1982), Roundup was more effective in identifying connected stems (73% response) than Weed-B-Gon (27% response).

The number of connections per treated stem did not vary with the age of the treated stems, but stem size was a factor. Herbicide symptoms generally appeared on connected stems that were smaller than the treated stems (fig. 8), suggesting a source-to-sink dilution of herbicide as it was translocated through root connections to larger stems. Height, basal diameter, and branch numbers of connected stems were all significantly ( $P = 0.05$ ) smaller than in treated stems:

	Height (m)	Basal Diameter (mm)	No. Branches
Treated Stems	1.44	19	12.3
Connected Stems	0.82	11	6.9

Excluding stems on the same node, the average distance between treated stems and connected stems exhibiting herbicide symptoms was 0.59 m.

## Discussion

The growth patterns observed in this study suggest that aspen ramets in stands regenerated by clearfelling



continue to function as integrated clonal units for some time. Although ramets appear to grow and compete as independent individuals, functional root connections continue to exist between some ramets.

The shift to independent growth and competition among ramets seems to occur between 8 and 14 years of age. Significant increases in height and biomass also occur during this period of time. Dominant stems which are only slightly larger than their subordinate neighbors during their first year or two of life begin to compound that advantage by 8 years of age. Corresponding increases in the average leaf area per stem result in a dramatic increase in LAI by age 8, since stem densities have stabilized by that age. The LAI of 4 observed in the 14-year-old populations is approaching the range of equivalent single surface LAI previously published for mature aspen (LAI = 5-10, Kaufmann et al. 1982).

The young aspen populations studied here did not exhibit the uniformly dense spacing associated with species that follow a phalanx clonal growth strategy (Lovett Doust 1981). Stems were not uniformly, or normally spaced, even in extremely dense 1-year-old stands, but were concentrated at root nodes that, in turn, were also aggregated. Although the degree of aggregation diminished somewhat with age, populations remained highly aggregated.

The huge reduction in stem density observed between 1 and 3 years of age occurred in a pattern suggesting that all stems at a root node die at the same time. The exponential decline in node density was very similar to the overall decline in stem density, but only a twofold decrease in the average number of stems per node had occurred by age 14. This indicates that stem mortality coincides with root node mortality as populations age, with the greatest mortality occurring among closely adjoining stems sharing the same parent root node during the first year or two following suckering. However, there is no way of knowing from this study whether or not root nodes actually died. These data only show that all of the suckers died at some nodes. The roots may still be functional via connections to other nearby suckers.

The herbicide experiment demonstrated that functional root connections exist between aspen ramets arising from a common root for at least 14 years following regeneration. Large stems appear to be functionally independent of each other at early ages, but small stems continue to be functionally attached to large neighbors. These connections might be a liability to the supporting ramets, but could also be beneficial. If a supporting stem dies, dependent stems will have a head start over competing vegetation in capturing space and resources relinquished by the dying ramet.

These results are not consistent with previous studies that reported a decrease in functional root connections among aspen ramets as clones age (DeByle 1964;

Jones and DeByle 1985; Maini 1968; Tew et al. 1969). There was no significant difference in the average number of suckers connected to herbicide-treated suckers among age classes studied here.

Zahner and Debyle (1965) severed root connections between dominant and subordinate stems of *Populus grandidentata* Michx. and observed reduced growth in the younger subordinates. They concluded that younger subordinates were dependent upon the older dominants. Although a similar pattern was evident in the herbicide study, the effect was more likely due to a source-to-sink dilution of herbicide. Stems of equal size or larger than the treated stems apparently did not receive a lethal dose of herbicide through the connecting root. An exception was in the 1-year-old population where the herbicide killed connected stems of all sizes (fig. 8). These fast growing ramets are apparently more sensitive to herbicide dosing through connecting roots. This may or may not indicate a greater dependency upon shared root resources.

Similar patterns of density decline and population aggregation among sparse and dense populations of increasing age indicate that these processes operate independently of population density. Mechanisms of self-thinning appeared to be operating in both dense and sparsely stocked populations, but they were more pronounced in dense stands. Conversely, differences in average stem height, leader length, and branch numbers between sparse and dense populations indicate that density does affect stem growth. Differences in the incidence of browsing between sparse and dense populations reflect the effects of increased animal access in sparsely stocked populations. Because they grow slower, sparse populations will also be subjected to the injurious effects of herbivory for a longer period of time.

The crown stratification patterns observed in these populations indicate that in spite of root connections among ramets, light-capturing ability still seems to determine whether a ramet will ultimately survive in the population. Subordinates may persist by sharing assimilates via root connections, but their slow growth places them at a higher risk of mortality as the population ages. This is especially true of subordinates that are closely aggregated beneath dominants. The mean number of stems per node in this study decreased slowly over time, indicating that smaller stems on a node may eventually succumb, in spite of the root connection.

## Conclusions and Management Implications

The role played by the lateral root system in vegetatively regenerating aspen seems to be much more comprehensive than the immediate reestablishment of the genotype. These studies indicate that parent root sys-



tem characteristics influence the development of the new stand for some time after stands are regenerated.

Root connections between aspen ramets arising from a single parent root appear to function for at least 14 years following regeneration by clearfelling. Although earlier literature has reported a reduction of root connections among suckers over time, the average number of root connections observed here between herbicide-treated suckers and other ramets did not diminish in the older populations.

Parent root nodes strongly affect the character and development of young aspen. Ramets are not randomly distributed in young aspen populations, but aggregate at root nodes that, in turn, are also aggregated. A ramet's success is keyed not only to its ability to compete with its neighbors, but also to the parental root node it occupies. While some mortality occurs among suckers sharing a root node, much of the exponential reduction in population density results when all suckers sharing a node die. This mode of density reduction causes the aggregation of individuals within the population to persist as they age. It also means that the fates of connected ramets are linked. They are more likely to survive or fail as a group, rather than individually.

As ramet populations age, surviving stems appear to become increasingly independent, even though root connections remain. Biomass, leaf areas, and crown stratification increase dramatically between 8 and 14 years of age. Larger stems overtop and dominate their smaller neighbors, even those sharing the same node or connected by a common root.

All of these processes appear to operate similarly in dense and sparsely stocked populations. Although poorly stocked stands have greater damage and reduced growth, their occurrence might be more closely related to the condition of the parent root system prior to regeneration. Additional research is needed to determine why the initial density of suckering root nodes is much lower in these stands.

Aspen's large woody growth form and its longevity make it much different than most of the clonal plants that have previously been studied. Clonal dynamics within aspen populations operate on a much larger spatial scale and for a much longer time than any examples of the phalanx or guerilla strategies described by Lovett Doust (1981). However, parent root systems certainly influence the growth, spacing, and development of ramets during the 14-year time period examined here and probably continue to influence growth throughout the clonal life cycle.

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Shepperd, Wayne D. 1990. Initial growth, development, and clonal dynamics of regenerated aspen in the Rocky Mountains. Res. Pap. RM-312. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 8 p.

Density, aggregation, crown stratification, and stem growth of 1- to 14-year-old aspen populations were utilized to investigate the role of root connections and clonal behavior in developing aspen. Evidence indicates that aspen ramets remain functionally connected through age 14, but become increasingly independent of the parent root system as they age. Density of stems and suckering root nodes declined exponentially over time with most mortality occurring by age 3. Individual stem biomass, leaf area development, and population leaf area index increased sharply from 8-14 years of age. Growth was strongly dependent upon crown position. Ramets were not uniformly distributed, in either dense or sparsely stocked populations.

**Keywords:** Vegetative regeneration, stand growth, coppice silviculture, root connections, *Populus tremuloides*



Rocky  
Mountains



Southwest



Great  
Plains

U.S. Department of Agriculture  
Forest Service

## Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

### RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

### RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico  
Flagstaff, Arizona  
Fort Collins, Colorado \*  
Laramie, Wyoming  
Lincoln, Nebraska  
Rapid City, South Dakota

\*Station Headquarters: 240 W. Prospect Rd., Fort Collins, CO 80526